Ecology of bats and their role in emerging zoonotic diseases: a review

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R. Biswas [(1)*], C. Debnath [(1)], I. Samanta [(2)], R. Barua [(1)] & A.D. Singh [(1)]

(1) Department of Veterinary Public Health, West Bengal University of Animal and Fishery Sciences, Kolkata–700037, West Bengal, India

(2) Department of Veterinary Microbiology, West Bengal University of Animal and Fishery Sciences, Kolkata–700037, West Bengal, India

*Corresponding author: dr.ripanbiswas@gmail.com

Summary

The order Chiroptera is the second largest order of mammals and shows great physiological and ecological diversity. These animals contribute significant ecological roles as prey and predator as well as facilitating pollination, seed dispersal, arthropod reduction and nutrient distribution and reutilisation in nature. Bats act as hosts to a range of viral, bacterial, fungal and parasitic zoonoses. Human activities increase the likelihood of exposure to bats, thereby increasing the opportunity for infections to spill over. Continuing ecological processes, emergence and spillover of novel pathogens in naïve hosts, including humans, along with other complex natural phenomena require proper understanding that may help in predicting the next spillover. This review will discuss the ecology of bats and their role in the emergence of different zoonoses, particularly those of viral origin, in an organised manner to increase understanding of the factors that may play significant roles in spillover of these pathogens from bats to other animals, including humans.

Keywords

Bat – Ecology – Emerging diseases – Epidemiology – Zoonoses.

Introduction

Bats are the only known flying placental mammals and they exist throughout the world excluding the Arctic (although a few species are present up to the Arctic Circle), Antarctica and a few oceanic islands. Around 75% of emerging infectious diseases (EIDs) of humans are zoonotic in nature, and a considerable proportion is derived from wildlife hosts such as bats (1). There are reportedly 1,314 genera and 6,495 species of placental mammals, among which bats are the second largest mammalian group next to rodents (2, 3). Taxonomically, bats are grouped in the order Chiroptera (in Greek '*cheir*' means hand and '*pteron*' means wing), which is classically divided into two sub-orders: Megachiroptera and Microchiroptera. The order Megachiroptera comprises only a single family while the Microchiroptera consists of 17 families of echolocating bats (echolocation is used for navigation and finding prey). However, the most comprehensive phylogenies of all Chiroptera suggest the presence of two basal groups, namely Yinpterochiroptera (consisting of 7 families of bats) and Yangochiroptera (consisting of 14 families). Presently, about 1,386 species of bats in 227 genera have been recognised (2). Microchiroptera use their larynx to create ultrasound and emit it through the mouth and sometimes the nose. The natural history of bats along with their physiological adaption, ecology, biology and evolution differentiate them from other mammals (3). The ability of these unique mammals to act as the reservoir hosts or vectors of different zoonotic diseases requires thorough investigation.

Although bats contribute to diverse ecosystems as pest controllers (insectivorous bats) and pollinators (frugivorous bats), their potential for disease transmission cannot be ignored (4). It is now clear that bats have been significantly underappreciated as reservoirs of viruses important to human and animal health. However, they seem to have a similar proportion of viruses per host species to other mammalian

orders (5, 6). Bats have evolved at a slow pace when compared with mammals of other taxa (7). They are exceptional among mammals in their ability to fly in search of food, and many species of bats fly long distances during seasonal migrations (8). Their size and weight are highly variable: their body weight ranges from 2 g in the bumblebee bat, the smallest mammal, to more than 1 kg in flying foxes such as *Pteropus* spp., whose wingspans can reach nearly 2 m (4, 9). Most bats hang upside down from their feet, a posture known as roosting, although some species just rest on the surface of the support without hanging (10); most bats can only crawl awkwardly on the ground. Owing to the small size and light weight of most bats, blood generally does not rush to their heads when they are roosting.

The lifespan varies among species, with the longest lifespan of approximately 41 years recorded for a Brandt's bat (*Myotis brandtii*; 5–10 g) from Siberia, based on recapture data (11). This prolonged lifespan encourages continuous viral replication, resulting in multiple horizontal and vertical transmission events through several generations, thus allowing virus conservation within populations over time (12). Most small mammalian species, including rodents, have evolved a 'live fast, die young' strategy, characterised by rapid reproduction and high mortality. In contrast, bats generally have a longer lifespan with multiple reproductive events, low litter size and delayed onset of sexual maturity along with different atypical sexual behaviours. All these traits favour the persistence and propagation of different pathogens. The higher body temperature of bats when active (which may be due to their flying ability and higher metabolic rate), in comparison with other terrestrial animals, creates an opportunity for them to act as vectors of a number of pathogenic organisms, particularly viruses.

Many pathogens survive in bats without showing pathogenicity, with a few exceptions such as rabies and rabies-related lyssaviruses. In a favourable ecological niche these viruses may be shed and spill over to other terrestrial animals, including humans, resulting in either an epizootic or an epidemic. The transmission route is, however, often not well understood. Many emerging pathogens, especially viruses

such as Hendra virus (HeV), Nipah virus (NiV), Ebola virus (EBOV), Marburg virus (MARV), severe acute respiratory syndrome coronavirus (SARS-CoV), Middle East respiratory syndrome (MERS) virus and, most recently, severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2), are of concern because they have high transmissibility and infectivity.

Outside tropical areas, bats go into hibernation in winter. This is an extended period of deep inactivity (torpor, different from sleep) that allows bats to survive cold winters with harsh weather and lack of food. A bat's body temperature lowers and its metabolic rate slows, resulting in a lower immune status and rendering it more susceptible to many known or unknown opportunistic microbes. While a bat is arousing from hibernation, which is a stressful event, many viruses that remain as latent infections may be reactivated.

Bats have a distinctive life history strategy for mammals of their size. Typically only a single infant is produced, although twins are common in some species that have multiple reproductive events. Owing to their long lifespan, this multiple gestation along with lactation and postnatal care augments stress. Furthermore, large colonies and multispecies associations are frequent among cave-dwelling bats, in particular during the maternity period. This colonial behaviour confers thermodynamic and social advantages on reproductive females during pregnancy and lactation. These factors allow bats to play a pivotal role in the epidemiology of a number of viral pathogens responsible for a similar number of emerging and re-emerging infectious diseases of humans and other animals (13). This review summarises and critically analyses the current knowledge on the aspects of bat biology, evolution, distribution and ecology that make them unique among mammals and permit them to be reservoirs of several emerging and re-emerging zoonotic diseases. Knowledge of the ecological aspects of bat-borne diseases is important in predicting future spillovers of those pathogens to humans and livestock. This may also help to prevent stigmatisation of bats and protect them from unnecessary and counterproductive culling as a result of fear, although the challenge is great.

Bat immunology

Mammalian cells have evolved well-maintained pattern recognition receptors (PRRs) that sense pathogen-associated molecular patterns (PAMPs) resulting from viruses, bacteria and parasites. Bats have both an innate and an acquired immune response, with similar immune organs, tissues, cells and immunoglobulin types to other mammals, although with some unique differences (14). The metabolic rate is higher in bats than in other mammals, thus the body temperature is also higher in bats, because of evolution of the mitochondrial deoxyribonucleic acid (DNA) damage and repair pathways (15). In bats, the DNA repair and DNA damage signalling pathways are maintained throughout their lifespan. Among DNA repair pathways, DNA double-strand break repair shows the strongest correlation with longevity. There are a number of DNA double-strand break repair genes which are under positive selection in some bat species. Bats may differ from other mammals in having a greater dependence on innate immunity than on adaptive immunity; innate immunity responds more readily than adaptive immunity, possibly allowing clearance of viral infections earlier than in humans.

The evolution of flight in bats has been complemented by genetic changes to their immune systems that allow high metabolic rates (16). Energetic demands associated with flight in bats require enhanced mitochondrial respiratory metabolism, which is expected to generate excess oxidative damage. To counteract this damage, bats have evolved more efficient mitochondria that produce less hydrogen peroxide per unit of oxygen consumed. To maintain proteostasis under oxidative stress, bats express high levels of major heat shock proteins that simultaneously permit them to endure high temperatures during flight and maintain protein homeostasis with age. Interestingly, it has also been reported that autophagy is enhanced with the advancement of age, resulting in further protection against viruses (17).

As mentioned earlier, roosting ecology permits increased exposure to pathogens, which help to influence immune defence. The adaptations found in the toll-like receptors (TLRs) among bat groups and

differences between the TLRs of bats and other mammals may aid in resistance to infections involving specific pathogens found in different environments (18). Bat interferons (IFNs) are only distantly related to those of humans and other mammals; the Type I IFN genes of bats are under positive selection and diversity is due to duplication and gene conversion (19). One remarkable difference between bats and terrestrial mammals is the loss of the interferon-inducible protein, also known as absent in melanoma 2 (AIM2), and gamma-IFN-inducible protein 16 (IFI16) genes which recognise microbial DNA, possibly reducing the sensitivity of bats to bacteria (20). Interestingly, many bat species display a daily period of torpor by decreasing their body temperature, which may be a method of virus resistance, interfering with optimal virus replication. There remain a number of questions that need to be answered in relation to bat immunology in order to explain why bats have been found to be a frequent source of human pathogens in recent decades (15).

Bat–human relationships

For bat-borne diseases to be established in humans, direct or indirect contact must occur to allow the disease to emerge and spread. These diseases are due not only to natural synanthropic association but also to a whole complex of factors related to biology, ecology, behaviour, landscape evolution and human intervention. Increased contact poses a challenge for both health experts and conservationists in the task of avoiding spillover of possible pathogens from wild animals to humans and livestock, while protecting wildlife and their habitats. The One Health approach is intended to promote, improve and protect the health and well-being of all species by increasing cooperation and collaboration among physicians, veterinarians and environmental experts. Bat viruses have been connected with diseases of humans, livestock and wild animals. The dramatic appearance of newly recognised viruses causing fatal diseases is a great challenge to the scientific and medical communities (21).

Bat–zoonosis nexus

Bats are recognised as significant reservoirs of zoonotic viruses (22). Attention is currently being paid to them because human intrusion into previously unfrequented natural areas is on the rise, mainly due to the biological richness of these areas and the growing demand for materials (23). So far, more than 200 viruses have been identified in bats (24), but only a few bat species have been recognised or suspected to be reservoirs of infectious zoonotic agents. Given that bats have the second highest population size among mammals, different human activities such as hunting bats for food, consumption of bush meat, agricultural and livestock practices that attract bats and penetration of bat habitat by humans may lead to spillover events from bats and outbreaks of different emerging and re-emerging diseases (25). In recent years, bats have been implicated in several EIDs and are progressively recognised as important reservoir hosts for emerging and re-emerging viruses which cross species barriers to infect humans and domestic as well as other wild mammals (5, 6). Numerous infectious diseases of humans and other animals are ecologically linked to bats. This review covers only the emerging and re-emerging infectious viral zoonoses linked to these species.

Rabies virus (RABV)

This group of negative-sense, single-stranded ribonucleic acid (RNA) viruses has been classified in the virus order Mononegavirales, family Rhabdoviridae and genus *Lyssavirus*. They replicate in the mammalian central nervous system and cause the disease known as rabies. Presently, the genus includes 16 documented viral species which are divided into rabies lyssavirus and the rabies-related lyssaviruses (15 species) (26). Rabies is estimated to cause 59,000 human deaths per annum in over 150 countries, with 95% of cases occurring in Africa and Asia. According to the World Health Organization (WHO), 99% of rabies cases are dog mediated and the burden of the disease is disproportionately borne by poor rural populations, with about half of the cases in children under 15 years of age. Dog-mediated rabies has been eradicated from Western Europe,

Canada, the United States of America (USA), Japan and some Latin American countries. With the eradication of terrestrial rabies in companion animals throughout North America, the transmission of rabies virus (RABV) to humans from bats has become more visible (27).

Bat-mediated rabies is recognised as causing the majority of human rabies cases in the Americas. Lyssaviruses may have evolved in bats long before the emergence of rabies in carnivores (28). The name rabies induces fear because the disease is associated with a fatality rate of 100% following the onset of the clinical disease in humans (29). Vampire bats (*Desmodus rotundus*), which are mainly found in the Caribbean and in Central and South America, have introduced a fear of rabies into human populations. At the same time they have driven an irrational and unjustified fear of bats across many cultures (30). Classical rabies virus has been reported in bats across North, Central and South America (27, 31) and was linked with vampire bats for the first time immediately after an outbreak in cattle in South America in 1911 (32). Bites from vampire bats are predominantly responsible for transmitting the disease to humans and domestic animals in Mexico and in Central and South America (33). In addition, between 1951 and 2006, Canada and the USA recorded 51 human rabies cases transmitted mostly by silver-haired bats (*Lasionycteris noctivagans*), eastern pipistrelle bats (*Perimyotis subflavus*) and Brazilian–Mexican free-tailed bats (31, 34).

Given that the vampire bat is not migratory, the spread of rabies in this species is mainly due to infected bats of one colony interacting with susceptible individuals from another overlapping colony. Rabies outbreaks caused by vampire bats can spread 5 km to 10 km per year; moreover, the direction of spread depends on the population density of bats in surrounding colonies (35). Rabies among bats is probably maintained via transfer of infectious saliva during licking, biting, ingesting regurgitated blood and perhaps by inhaling aerosolised saliva (36). Close bat–human interactions, including the sharing of living spaces and hunting and butchering of bats for food and medicines, may lead to spillover of virus into human populations.

Spillover from bats is observed only with RABV in the Americas (37). It is noteworthy that an unvaccinated adolescent has survived, after developing rabies from contact with a bat, with novel therapy known as the 'Milwaukee protocol' (38).

Other lyssaviruses related to rabies

There are seven lyssavirus genotypes, and an additional four novel genotypes recently recorded from bats in Eurasia may be included in this genus (39). Among them, the most widely reported are European bat lyssavirus type 1 (EBLV-1) and European bat lyssavirus type 2 (EBLV-2); they have been frequently detected in serotine bats (*Eptesicus serotinus*) and Daubenton bats (*Myotis daubentonii*), respectively (40). Between 1977 and 2011, a total of 961 cases of bat rabies were reported to the WHO Rabies Bulletin Europe, with the vast majority (> 97%) being attributed to EBLV-1 mainly from the Netherlands, Denmark and Germany. It is interesting to note that the first EBLV-2 case, reported in the United Kingdom, began a debate on the rabies free status of that country (41, 42). Aravan virus (ARAV), Irkut virus (IRKV), Khujand virus (KHUV) and West Caucasian bat lyssavirus (WCBL) were described following extensive phylogenetic analysis of single isolates of each type from various bat species (43). After the first human case, reported in 1970, another two fatal human infections involving Duvenhage virus (DUVV) have been reported, one in South Africa in 2006 (44) and one in the Netherlands in 2007, in which the patient contracted the infection in Kenya (45). In Africa, Lagos bat virus (LBV) has been isolated from a variety of fruit bat species, one insectivorous bat species, domestic cats, domestic dogs and a water mongoose, but not humans (31). In 1996, Australian bat lyssavirus (ABLV) was first reported in a black flying fox, and a 39-year-old woman died with clinical rabies after being bitten by a yellow-bellied sheath-tail bat (46). Another two human cases have been reported, in a woman scratched and a child bitten by flying foxes.

Hendra virus (HeV) disease

Hendra virus is a novel paramyxovirus (genus: *Henipavirus*) responsible for serious illness and death in horses and humans; HeV is endemic in Australia only because of flying foxes. It was first recognised in September 1994 during an outbreak of acute respiratory disease in horses in a place called Hendra, close to Brisbane, Queensland, Australia (47). In this outbreak, 13 of 20 infected horses died or were euthanised; two humans (a horse trainer and a stable hand) who worked closely with the horses became infected, and one died of acute pneumonia (48, 49). The initial name of this novel virus was equine morbillivirus (EMV), but it was later renamed HeV (50). The virus was transmitted to humans through an intermediate equine host from bats of the genus *Pteropus*, which are colloquially referred to as flying foxes (51). There have been 31 documented spillovers of HeV, with a total of 66 recognised equine cases and 7 human cases resulting in 4 human deaths (52). In July 2013, during investigation of HeV infection in a horse near Macksville, New South Wales, Australia, infection was also detected in a dog on the same farm (53). Transmission from horses to humans results from close contact with horses, during post-mortem examination, husbandry and veterinary procedures, and is thought to occur via respiratory droplets, cuts and abrasions of mucous membranes. The mode of transmission of HeV from bats to horses has not been fully explained, but is hypothesised to involve ingestion of contaminated food or contact with contaminated surfaces (54). The virus has been identified in the birthing fluids, placental materials and aborted pups of flying foxes. As HeV is often detected in the urine of wild flying foxes (55), the principal routes of transmission to horses are thought to be via material recently polluted with bat urine or direct transmission (56). Bat urine appears to be the most important source of this virus, with other secretions and excretions (e.g. faeces, nasal and oral secretions) less significant in transmission. The detection of antibodies in flying foxes in Papua New Guinea may be linked to HeV or a similar virus. Transmission of the virus among horses appears to be more likely with horses kept in close proximity; for example, companion horses in stalls have also been infected. No evidence of human to human,

human to horse or flying fox to human transmission of HeV has been reported (57).

Nipah virus (NiV) disease

This is the second novel *Henipavirus* recognised within the Paramyxoviridae family to be associated with flying foxes. It was first described between September 1998 and April 1999 in pigs and pig farm workers affected by fever and encephalitis, some with respiratory illness, during a major outbreak in Peninsular Malaysia (58). In March 1999, a team of virologists from the University of Malaya, Kuala Lumpur, Malaysia, isolated a virus from a patient in Sungai Nipah (Nipah River village) and named it Nipah virus (NiV). This outbreak resulted in the death of 105 humans and the culling of more than 1 million pigs (59, 60). A similar outbreak was witnessed in the town of Sikamat, Negri Sembilan state, Malaysia, from December 1998 to January 1999, but the largest outbreak was observed in an adjacent area of Bukit Pelandok, Malaysia, in December 1998 (61). This new disease was initially considered to be Japanese encephalitis (JE), which is generally prevalent in these areas (59). Most of the humans affected in the Malaysian outbreak had a history of direct contact with live pigs, and most were adult male Chinese pig farmers (62). Following importation of infected pigs from the infected area of Malaysia the infection spread to Singapore. Eleven human cases were confirmed in Singapore with one death. Spillover of NiV has not been observed since this time in Malaysia or Singapore. Malaysia has a great variety of bat species, including 13 species of Megachiroptera and 60 species of Microchiroptera; among them, the large flying fox (*Pteropus vampyrus*) and the variable flying fox (*Pteropus hypomelanus*) were found to be natural reservoir hosts for NiV (63).

The disease was also reported in Bangladesh, initially in 2001. The Institute of Epidemiology, Disease Control and Research (IEDCR) in Bangladesh reported on their website, from April 2001 to January 2020, a total of 319 human cases which were found to be positive for NiV in repeated outbreaks, and 225 deaths. In Bangladesh, none of the human cases was connected with disease in pigs, and there was some

evidence suggesting human to human transmission (64). An important epidemiological factor in the transmission of this disease in Bangladesh has been recognised to be the consumption of date palm sap contaminated by bat saliva (65). However, washing of infected corpses before burial according to Islamic custom may be another means of transmission among family members (66). Contact with domestic animals and climbing trees were shown to be less important risk factors for infection (67). The risk of direct human infection with NiV from bats has been shown to be lower than the risk of horizontal transmission once the virus enters the human population (68).

During 2014, a total of 17 laboratory confirmed cases of NiV, with 9 deaths, were reported from the southern part of the Philippines, where horse to human as well as human to human transmission events were observed and flying foxes (*Pteropus* bats) were found to be most likely to be responsible for the infections (69). Since 2001, three outbreaks of NiV have been reported in India, where the first outbreak was in Siliguri, West Bengal state, with a total of 66 confirmed cases and 45 deaths. The second outbreak, in 2007, was in Nadia district in the same state (70), with a total of 30 confirmed cases and 5 deaths. The third and final outbreak, in May 2018, was noted in Kozhikode and Malappuram districts of Kerala, with 17 deaths and a total of 35 confirmed cases (71). The 2018 outbreak originated in three members of a family who died after cleaning an old deep well inhabited by bats.

Cedar virus (CedPV) disease

A non-pathogenic *Henipavirus* species was identified in urine samples from *Pteropus alecto* and *Pteropus poliocephalus* in Australia in 2012. It seems to have low pathogenicity and failed to produce clinical signs in laboratory animal species (72).

Menangle virus (MenPV) disease

In 1997, this paramyxovirus of pteropid bats was identified in stillborn piglets during the study of a severe outbreak of reproductive disease on a pig farm in New South Wales, Australia. Two humans who had a history of close contact with infected pigs were shown to have

neutralising antibodies to Menangle virus during the serological investigation (73).

Tioman virus (TioPV) disease

A novel paramyxovirus was identified during the search for the reservoir host of NiV on Tioman Island, off the eastern coast of Peninsular Malaysia (74). Pigs are reported to be susceptible to Tioman virus and neutralising antibodies to this virus have been identified in humans, suggesting prior exposure to or infection with the virus (75).

Ebolavirus (EBOV) disease

This virus belongs to the family Filoviridae of negative-stranded RNA viruses; the genus *Ebolavirus* causes life-threatening disease with mortality rates ranging between 30% and 90% and is endemic in regions of West and Equatorial Africa (76). It is also known as Ebola haemorrhagic fever as the disease is mainly characterised by abnormal bleeding both internally and externally. The name 'Ebola' is derived from a river in the Democratic Republic of the Congo (DRC, previously Zaire) in Africa, where it was first documented in 1976 (77). Ebola haemorrhagic fever is caused by any of five genetically distinct viruses: Zaire Ebolavirus (ZEBOV or EBOV), Sudan Ebolavirus (SEBOV or SUDV), Ivoire Ebolavirus (Taï Forest Ebolavirus, TAFV), Bundibugyo Ebolavirus (BDBV) and Reston Ebolavirus (REBOV or RESTV) (78). Human infection is mainly associated with Bundibugyo, Sudan and Zaire Ebolaviruses, which are responsible for different outbreaks, but Zaire Ebolavirus has been found to be a serious hazard to both human and non-human primates in Sub-Saharan Africa. Ivoire Ebolavirus was confirmed in Côte d'Ivoire in only one human case, which was non-fatal; the patient had a history of travelling from Liberia to Sierra Leone (79). Reston Ebolavirus is considered to be non-pathogenic to humans but pathogenic to non-human primates (monkeys, gorillas and chimpanzees) and has been isolated from pigs with porcine reproductive and respiratory disease (76). Some Ebolaviruses circulate among fruit bats (*Hypsignathus monstrosus*, *Epomops franqueti* and

Myonycteris torquate) (80), from which these viruses may be transmitted to their intermediate hosts, non-human primates, so that bats and simians may act as sources of infection during handling or consumption by humans. Human to human transmission is possible through direct contact with mucus, saliva, urine, vomit, faeces, breast milk, sweat, tears, semen and infected live or dead human bodies (81). Sexual transmission has been reported to occur from recovered patients. In Ebolavirus disease outbreaks, the following death rates have been reported: 88% in 1976, 81% in 1995, 73% in 1996, 80% in 2001–2002 and 90% in 2003. The most devastating outbreak was reported in West Africa between 2014 and 2016, where more than 20,000 cases were reported, with the deaths of over 11,000 people giving a case fatality rate ranging between 28% and 74.2% (82). Since the first outbreak, more than 20 documented outbreaks of Ebola disease have been reported in Sub-Saharan Africa, predominantly in Sudan, DRC, Uganda and Gabon. Ebolavirus disease outbreaks have generally been confined to African countries, with some spread to adjacent countries. During the latest outbreak, in January 2020, a total of 12 cases were reported in DRC. The disease has also been reported in Spain (one confirmed case) and the USA (four confirmed case), though the patients had a history of travel in African countries with a link to the large West African outbreak (83).

Marburg virus (MARV) disease

This infectious agent was first observed in August 1967, when laboratory workers were infected in Marburg and Frankfurt, Germany and Belgrade, Serbia. It is a member of the Filoviridae family, which includes the genera *Ebolavirus*, *Marburgvirus*, *Striavirus*, *Cuevavirus* and *Thamnovirus* (84). African green monkeys (*Chlorocebus aethiops*) that had been imported from Uganda to Marburg, Frankfurt and Belgrade were the source of the infection. Egyptian fruit bats (*Rousettus aegyptiacus*) act as the main natural reservoir host (85), although several bat species have been recognised as hosts of filoviruses. In the second episode, in 1975, the primary human case was in a young Australian, who was hospitalised in Johannesburg, South Africa, after travelling throughout Zimbabwe; the isolated virus

was similar to that reported in Germany. The disease has also been reported in Kenya, first in 1980 and subsequently in 1987 (85).

Severe acute respiratory syndrome coronavirus (SARS-CoV) disease

This virus belongs to the genus *Coronavirus* in the family Coronaviridae, which comprises pleomorphic, enveloped, positive sense and single-stranded RNA viruses with a nucleocapsid of helical symmetry. In November 2002, the first known case was reported in Foshan, Guangdong Province, People's Republic of China (China). A pandemic (involving 33 countries) started in November 2002 and was brought under control in July 2003, involving 8,422 cases and 916 fatalities (86, 87). In March 2003, a novel coronavirus, SARS-CoV, was identified from sequences obtained from patients with severe acute respiratory syndrome (SARS) (88). Restaurant workers handling wild animals as exotic food in Guangdong Province were reported to have been early cases (89). A virus similar to SARS-CoV was isolated from Himalayan palm civets (*Paguma larvata*) and racoon dogs (*Nyctereutes procyonoides*) sampled from marketplaces. After that, the palm civet caught the attention of the scientific community because sporadic primary cases occurred in persons associated with restaurants in which palm civet meat was prepared and consumed (90). Moreover, when culling of palm civets in Guangdong marketplace was performed as a preventive measure, a dramatic reduction in cases was noticed after the winter of 2003–2004, which suggested that these animals were the source of the spillover. In addition, SARS-CoV was reported in cats, red foxes and Chinese ferret badgers (antibodies only) sampled in marketplaces.

Viruses similar to SARS-CoV have been isolated from several bat species, predominately horseshoe bats (genus *Rhinolophus*), which act as natural reservoirs. The appearance of a zoonotic virus from a wild animal reservoir involves four factors: *a)* interspecies contact, *b)* cross-species virus transmission (spillover), *c)* virus adaptation in the spillover species and *d)* constant transmission. All these factors were thought to be present during SARS outbreaks and helped to

spread the infection rapidly to several countries (91). After the abrupt ending of the SARS-CoV pandemic in July 2003, no human cases have been detected in the past 18 years.

Middle East respiratory syndrome coronavirus (MERS-CoV) disease

In April 2012, Middle East respiratory syndrome coronavirus (MERS-CoV), a deadly zoonotic pathogen, was first identified in a lung sample from an adult human patient hospitalised in Jeddah, Saudi Arabia who had severe pneumonia and died of multi-organ failure. Between April 2012 and the end of December 2019, MERS-CoV infection was associated with 858 deaths among 2,499 confirmed human cases in 27 countries (92), but the majority were documented in Saudi Arabia (2,106 cases, 780 deaths). The MERS-CoV is closely related to coronaviruses found in Asiatic bats, suggesting that bats may be a reservoir of MERS-CoV, although no evidence of antibodies to MERS-CoV has been found in bats (93). Dromedary camels act as the intermediate hosts of MERS-CoV but the evolutionary path is not clear (94). In 2013, a camel was reported to have developed clinical signs of MERS-CoV, displaying fever and rhinorrhoea, although bats are supposed to be carriers that show no clinical signs of the disease. Human to human transmission is observed but is limited to close contacts and family members, or associated with nosocomial infection (95). Camel to human transmission of MERS-CoV has been documented in Saudi Arabia. Multiple disease transmission events may result from intensive camel rearing and the large camel trade (roughly 77,000 live camels are transported each year between countries, mainly from Somalia to the Gulf region).

Severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) disease

The 2019 novel coronavirus (2019-nCoV), now called SARS-CoV-2, spread from its origin in Wuhan City, Hubei Province, China to the rest of the world (96). On 11 February 2020, it was renamed SARS-CoV-2 and the disease caused by this virus was called ‘coronavirus disease 2019’ (COVID-19). Compared with SARS-CoV and MERS-

CoV, this virus has higher transmissibility and infectivity, despite a low mortality rate; the mortality rates of SARS-CoV and MERS-CoV were about 10% and 35%, respectively (97). The first case of pneumonia associated with SARS-CoV-2 was detected on 12 December 2019, and influenza and other coronaviruses were ruled out by laboratory testing (98). Many of the initial cases had a common exposure to the Huanan wholesale seafood market, which also used to trade live wild animals. On 22 January 2020, it was declared that the novel CoV may have originated from wild bats and the novel virus was found to be a Group 2 *Betacoronavirus*; this group also contains SARS-associated coronavirus. With the similarity of SARS-CoV-2 to bat SARS-CoV-like coronaviruses, it was suspected that bats act as reservoir hosts for its progenitor while pangolins (not proven) and snakes (very unlikely) were suggested but not confirmed to be the intermediate hosts (99). The Chinese Lunar New Year holiday, which coincided with the emergence of COVID-19, is the most celebratory time of year in China, during which an immense number of human movements (nearly 3.11 million people) take place as individuals travel back to their hometowns. On 11 March 2020, WHO declared the novel coronavirus outbreak, COVID-19, to be a pandemic. On 6 April 2021, 219 countries and territories had been affected, with a total of 131,487,572 human SARS-CoV-2 cases and more than 2,857,702 fatalities reported worldwide (100). The main route of transmission of the disease appears to be human to human transmission via droplets or by direct contact, and the infection has been estimated to have an average incubation period of 6.4 days (101). A Pomeranian dog from Hong Kong, a cat from Belgium and one tiger in a zoo in New York have been confirmed with COVID-19 to date, all contaminated by infected human beings.

Conclusion

From horror films to tabloid pages, symbolic images of bats are used to stimulate fear. However, bats are not our foes, as they play a significant role in many environments around the globe and the authors have a long history of co-existence with bats, in caves, huts, and log cabins. Many humans in Africa, Asia, the Pacific and Indian

Ocean Islands still hunt bats for food. Pollination of some plants depends partially or solely on various bats, while others help to control pests by eating insects. Bats act as seed dispersers and agents of re-forestation when seeds of the fruits they ingest are excreted in their faeces. Moreover, the guano of bats is used as fertiliser and in the manufacture of soaps, antibiotics and gasohol. Bats are an important part of our natural wildlife in which they play a significant role to maintain ecology as well as diversity. Although bats are the reservoir hosts of a variety of zoonotic pathogens, they differ from other mammalian reservoir hosts in their unique ability to fly, diverse lifestyles, long lifespan and low fecundity rate. On the one hand, bats are penetrating into human-dominated sites to find alternative food sources, owing to reduced habitat availability; on the other hand, the human habit of consuming bush meat, including bats, is aggravating the situation. As a result, the likelihood of spillover and direct transmission of emerging diseases is increasing with time. This narrative review has collated the latest available information in relation to bat ecology and emerging and re-emerging bat-borne viral zoonotic diseases from diverse sources, with the hope of supplementing the knowledge of public health professionals, researchers, academics, ecologists and similar stakeholders about this important partner in our planetary ecology. Unified attitudes, including in public health, ecology, and conservation biology, are desirable in understanding, combatting and preventing emergent diseases in bats.

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